Reading Theory Exercise

Theory for Everyone – ESA workshop – ESA Annual Meeting 2026

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Our goal is to get everyone to (1) engage critically with theory, (2) recognize that the results of a theory reflect only the assumptions that feed into it, and (3) begin thinking about the relevance of theory in their own work.

We have translated a few theoretical studies across different topics into digestible summaries. In groups, pick one of the studies to read together.

While reading, identify:

- The big picture, general research area and question.
- The general approach
- What goes in (the assumptions), what goes out (the analysis)
- The major findings of the analysis
- Do you buy it? How would you make it more applicable to your study system?

Discuss the guiding questions to check if you are thinking critically.

If time permits, do a second one!

Papers:

Metabolic interplay drives population cycles in a cross-feeding microbial community.
Ross, T.D., Im, H., Keogh, B.G. et al. 2025. Nature Communications 16, 8919.

The interaction between predation and competition.
Chesson, P. and Kuang, J.J., 2008. Nature, 456(7219), pp.235-238.

Impact of intraguild predation and stage structure on simple communities along a productivity gradient.
Mylius, S.D., Klumpers, K., de Roos, A.M. and Persson, L., 2001. The American Naturalist, 158(3), pp.259-276.

Effective leadership and decision-making in animal groups on the move.
Couzin, I.D., Krause, J., Franks, N.R. and Levin, S.A., 2005. Nature, 433(7025), pp.513-516.

Disclaimer: These summaries have been put together for educational purposes to practice the process of reading theoretical papers. There may be errors or omissions. Please refer to the original manuscripts for anything other than this exercise.

Ross, T.D., Im, H., Keogh, B.G. et al. 2025. Metabolic interplay drives population cycles in a cross-feeding microbial community. *Nature Communications* 16, 8919.

This paper investigates how a mechanism of mutualism may make a community resistant to cheating.

This study includes both empirical and theoretical work. The researchers start with an experiment with two strains of *E. coli*. Each strain produced an amino acid that the other strain could not produce but was essential to the other strain's growth. Thus, the two strains were part of a "cross-feeding" community. They also competed for necessary glucose throughout the experiment. When grown with no external amino acid supply, the population sizes of each strain stabilized at a single value. But when the communities were grown under a low supply of external amino acids, the population sizes exhibited sustained large-amplitude oscillations.

To test whether cross-feeding could cause this phenomenon of sustained oscillations in population sizes, they developed a model of the community. Their model includes the two strains, two cross-fed resources (amino acids), and one common resource (glucose) that ultimately limits the growth of the community. Each strain needs both amino acids and glucose to grow, but it only produces one amino acid. The growth rate of each strain is determined by its limiting resource: either the amino acid it needs or glucose.

Each strain produces their amino acid at a rate proportional to their glucose uptake. When the strain is glucose-limited, it doesn't release any amino acids into the environment. When glucose is saturating and the strain is limited by the amino acid it does not produce, it excretes the excess amino acid that it does produce to the environment.

The authors find that these simple assumptions do indeed lead to oscillations in population sizes without any externally driven variation in the environment.

Using the model, the authors show that within a cycle, the community switches between two metabolic states. In each state, one *consumer* strain is glucose-limited, so it does not release any of the amino acids it makes. The other *producer* strain is consequently limited by its required amino acid and therefore releases the amino acid it produces, which fuels the growth of the consumer. Finally, they also show that, due to the temporal separation of the dominance of the two producer strains, a cheater strain (which doesn't produce either amino acid but consumes both) cannot invade this community and ruin the mutualism. Therefore, they showed that cross-feeding mutualisms can be resistant to cheating through generating population cycles.

Questions to think about:

1. What is the exciting result about mutualisms from this research?
2. Can you apply that result to any mutualism of interest? Why or why not?
3. The researchers already demonstrated the existence of cycles through their experiments. What additional value did the model add?
4. Bonus question: why does the mutualism not result in a population explosion from the positive feedback between both species?

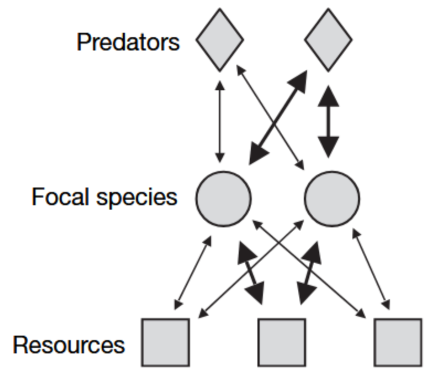
Scan the QR code or visit the link to view suggested answers:

https://farriorlab.github.io/theory-workshop/theory-papers/cross-feeding-microbes.html

Chesson, P. and Kuang, J.J., 2008. The interaction between predation and competition. *Nature*, *456*(7219), pp.235-238.

Past studies have shown that for two competing species to coexist, the competition within each species (intraspecific competition) must be greater than the competition between two different species (interspecific competition). The authors were interested in finding out how predation, in addition to competition, contributes to species coexistence through effects on the niche overlap (the effective similarities) of species.

To do this, the authors formulate a three-trophic-level model with two focal species (consumers), two predators of the focal species, and three resources that the focal species compete for. Each focal species increases in population size by consuming the resources, and decreases due to predation and natural mortality. Without the interactions, predators and resources follow logistic growth (increase from rarity up to a carrying capacity). Through their interactions with the focal species, predators increase and resources decrease.



The authors found that predation and resource competition can, in theory, affect focal species coexistence similarly. If focal species specialize on different resources but share the same predators, the authors find overall niche overlap decreases (and thus the likelihood of coexistence increases) with a greater relative importance of resources over predation. On the other hand, if focal species have distinct predators but share the same resources, the authors found that overall niche overlap decreases (and coexistence increases) with an increasing relative importance of predation.

Questions to think about:

1. Notice the assumptions of logistic growth by both resources and predators. The resources will increase rapidly if their abundance is close to zero, but cannot increase higher than a set carrying capacity. Is this a good characterization of a biotic or abiotic resource?
2. Two cases are mentioned in the last paragraph where niche overlap can be reduced. There is also a somewhat “trivial” case where niche overlap is even lower than those mentioned. What would that be? How does that promote coexistence?
3. Do you “buy” the insight that resource competition and predation may play similar roles in focal species coexistence? Are there missing differences between predation and competition in the model that you think could affect this insight?

Scan the QR code or visit the link to view suggested answers:

https://farriorlab.github.io/theory-workshop/theory-papers/predation-competition.html

Mylius, S.D., Klumpers, K., de Roos, A.M. and Persson, L., 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *The American Naturalist*, *158*(3), pp.259-276.

An expectation from food-chain theory is that increasing productivity in an ecosystem should allow more trophic levels to exist. These researchers ask whether this remains true when the top consumer is omnivorous and can feed on a shared resource as well as a fellow consumer (Fig. 1). This situation, known as intraguild predation, is common in nature.

The model contains three species: a basal resource (*R*), a prey species (*C*), and a predator (*P*). Both consumers (*C* and *P*) feed on the resource, but the predator can also consume the prey (Fig. 1). The prey (*C*) is assumed to be the superior competitor for the resource. Productivity determines the rate at which the resource is supplied to the system. The populations in the community are assumed to be well mixed. The researchers analyze the model to find the equilibrium abundances of the species for different values of ecosystem productivity. Specifically, they determine which species can persist at equilibrium and whether coexistence between the intraguild predator (*P*) and intraguild prey (*C*) is possible.

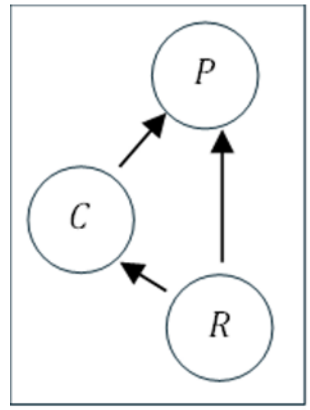


Fig. 1: Species P (intraguild predator) preys on the consumer C (also called the intraguild prey). Both the predator and the consumer compete for a shared basal resource R.

The authors find that coexistence of *P* and *C* is possible when productivity is intermediate. At low productivity, the intraguild predator does not have enough to eat to maintain a population. At high productivity, the predator becomes so abundant that it eliminates the intraguild prey through predation. But, with the same model mechanisms, at intermediate levels of productivity all three species coexist. Thus, the authors conclude, increasing productivity does not always promote more trophic levels. Instead, when intraguild predation occurs, the coexistence of all three trophic levels happens only over a relatively narrow

Questions to think about:

1. In a linear food chain with a primary producer at one end, there is an expectation that the greater the primary productivity, the longer the chain that it can support, i.e. the more trophic levels can coexist. Is that expectation consistent with this study?
2. Intraguild predation is commonly observed in nature, but the model also assumes that the consumer is the better competitor for the shared resource. Does that seem realistic? Might this assumption matter for the result?

3. Notice that the whole world for these species is *C*, *R*, and *P* alone. In a real food web with additional resources, prey, and predators, do you think these results would be likely to strengthen or weaken? Why?

Scan the QR code or visit the link to view suggested answers:

https://farriorlab.github.io/theory-workshop/theory-papers/intraguild-predation.html

Couzin, I.D., Krause, J., Franks, N.R. and Levin, S.A., 2005. Effective leadership and decision-making in animal groups on the move. *Nature*, *433*(7025), pp.513-516.

This paper investigates how schools of fish are capable of coordinated group movement. The authors are interested in whether a few informed individuals can lead a group when the movement of rest of the individuals is governed by simple rules of attraction and avoidance.

The authors simulate the direction of travel of each individual fish as a vector, influenced by the following factors. For uninformed individuals, their decision is purely based on social interactions – when too close to others (other individuals are detected within a small radius), the individual turns away from neighbors. When no neighbor is too close, the individual is attracted to and aligned in the direction of movement with the neighbors that are close enough to see (within a second larger radius). In this case, the direction of the fish is a compromise between going straight to the neighbors and heading in the same direction as them. Informed individuals follow the same rules, except that they follow a compromise between the direction they would have if they were uninformed (the social cues) and the direction of their information. A weighting factor determines how strongly the informed individuals follow their own information versus the social cues.

Through the rules of sticking together but not getting too close, the group can balance accuracy with the risk of group splitting, especially for intermediate proportions of informed individuals levels. The authors find that, for a given group size, accuracy (the deviation between the group direction and the informed direction) increases with the proportion of informed individuals. Interestingly, compared to smaller groups, larger schools of fish need a smaller proportion of informed individuals to achieve the same level of accuracy. Said another way, in some cases, adding additional uninformed individuals to these schools of fish can improve their accuracy.

The authors also investigate the case when different informed individuals have different information (and want to go different directions). In this case, the direction of the majority of informed individuals usually prevails. If the differing informed groups have the same size, the school travels in the average direction when the difference between the preferred directions is small, and switches to randomly choose one out of the two preferred directions when the difference is large.

Overall, this study uses a simple model to demonstrate how group decisions can emerge from localized interactions, and be influenced by multiple group properties. It has inspired a series of experiments and observational studies on fish and mammals to explore the role of uninformed individuals and group size in collective decision making: https://www.ab.mpg.de/414346/collective-decision-making

Questions to think about:

1. In this model, can uninformed individuals distinguish between other uninformed individuals and informed individuals? If you aren't sure, which of these assumptions would make the results stronger (that is, which assumption would make the results more relevant to real fish schools)?
2. In the scenarios where two informed groups have different preferred directions, what do you think would happen if the informed fish could adjust their behaviors, e.g. they put more weight on their preferred direction when the group is traveling in a similar direction and put less weight on their preference when it deviates from the group's decision?
3. Are there other systems where these assumptions might fit well enough for us to apply the insights here to their group decision making?
4. In this model, the only external source of information is the direction the informed individuals are aware of and are attracted towards. In reality, an external source of information may be repulsive instead of attractive, such as if informed individuals are repelled by a predator trailing the school of fish. Describe one way of implementing such a mechanism in the model so that the predator is always "chasing" the school of fish.

Scan the QR code or visit the link to view suggested answers:

https://farriorlab.github.io/theory-workshop/theory-papers/fish-movement.html